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Topographic and soil influences on root productivity of three bioenergy cropping systems

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Summary

- Successful modeling of the carbon (C) cycle requires empirical data regarding species-specific root responses to edaphic characteristics. We address this need by quantifying annual root production of three bioenergy systems (continuous corn, triticale/sorghum, switchgrass) in response to variation in soil properties across a toposequence within a Midwestern agroecosystem.
- Using ingrowth cores to measure annual root production, we tested for the effects of topography and 11 soil characteristics on root productivity.
- Root production significantly differed among cropping systems. Switchgrass root productivity was lowest on the floodplain position, but root productivity of annual crops was not influenced by topography or soil properties. Greater switchgrass root production was associated with high percent sand, which explained 45% of the variation. Percent sand was correlated negatively with soil C and nitrogen and positively with bulk density, indicating this variable is a proxy for multiple important soil properties.
- Our results suggest that easily measured soil parameters can be used to improve model predictions of root productivity in bioenergy switchgrass, but the edaphic factors we measured were not useful for predicting root productivity in annual crops. These results can improve C cycling modeling efforts by revealing the influence of cropping system and soil properties on root productivity.

Introduction

Root production plays a key role in ecosystem carbon (C), nutrient and water cycling, yet our scientific understanding of variability in root productivity over heterogeneous environmental conditions is not well developed (Pritchard & Rogers, 2000; Franklin, 2005). Characterizing spatial variation of root production is necessary for more precise estimates of C flux within a system (Harmon *et al.*, 2007), and serves to reduce uncertainty in ecosystem nutrient budgets (Lehrter & Cebrian, 2010; Yanai *et al.*, 2010). Moreover, knowledge of the impacts of environmental drivers on variation in root production is critical for upscaling measurements of primary production and biogeochemical processes to predictions over landscapes, regions and the globe (Turner, 2005) – scales meaningful to ongoing national and international discussions regarding climate and energy policies.

Improving our understanding of the impacts of bioenergy production on broad-scale carbon and nutrient cycling is paramount for the development of a sustainable bioeconomy (Jordan *et al.*, 2007), yet scaling root productivity estimates of agricultural cropping systems beyond plot scales poses significant challenges to researchers. Whether crops grown for bioenergy are annual or perennial will influence the biogeochemical cycling and the overall potential ecological benefit of these systems (Robertson *et al.*, 2011). The realized improvements in ecosystem functioning of these contrasting approaches may also differ with location in the landscape (Dale *et al.*, 2011; Gelfand *et al.*, 2013) according to variation in edaphic conditions such as soil physical properties and nutrient concentrations. For the development of cellulosic bioenergy to meet the dual goals of high energy output and reductions in greenhouse gas emissions, an understanding of how root inputs associated with bioenergy feedstocks vary in response to topographic and soil heterogeneity is needed (Taubert *et al.*, 2012).

Past work on the response of root growth to variation in soil properties at multiple spatial scales provides a foundation for this study. At broad scales, statistical models have the potential to improve our understanding of root productivity based on environmental variables such as mean annual temperature, aboveground biomass, and broad-scale patterns in soil nutrients (Gill *et al.*, 2002). For example, Yuan & Chen (2012) evaluated the response of root productivity to soil nutrients within 410 forests and grasslands distributed worldwide. Their cross-ecosystem analysis showed soil type and soil chemistry as having the strongest explanatory power, respectively explaining 28% and 22% of the variation in root production; among soil chemistry variables, root production increased in response to increasing nitrogen (N), phosphorus (P), pH and C. Such broad-scale pattern–process relationships, however, are the aggregate of root productivity responses to soil heterogeneity patterns at finer scales.

At the scale of an individual plant, roots generally respond to heterogeneity of soil resources by proliferating into nutrient patches (Fitter, 1987), given adequate soil moisture. However, this response is dependent on the plant species and nutrient demands or limitations (Hodge, 2004). Increasing silt and clay content affects the degree of soil bulk density that restricts root growth of annual crops (Jones, 1983; Unger & Kaspar, 1994) through impacts on soil strength and water potential (Dexter, 2004). Improved soil physical quality (e.g. decreased bulk density, increased porosity and soil organic matter (SOM) content) is manifested as increased aeration and water infiltration, reduced soil compaction, and increased root penetration and growth (Dexter, 2004).

While fine-scale plant–soil relationships provide a mechanistic understanding of root production, scaling information from individual plants to broad spatial extents such as landscapes, regions and continents requires knowledge of pattern–process relationships at intermediate scales (10–1000s m^2; Peters *et al.*, 2007). Soil properties have been shown to be spatially variable across fields and watersheds, corresponding to intermediate scales (Cambardella *et al.*, 1994; Garten *et al.*, 2007). Variation in edaphic properties can be linked to differences in soil type related to topography (Burke *et al.*, 1989; Cambardella *et al.*, 2004), which can influence the productivity of annual crops. For example, variation in topsoil depth at field scales significantly affects grain yields of corn (*Zea mays*; Jagadamma *et al.*, 2009), while SOM contents influence crop performance of corn across landscape positions in an agricultural watershed (Stott *et al.*, 2011).

Given the considerable plasticity of root systems to differing soil conditions, stand-level root productivity is predicted to vary with field-scale soil heterogeneity (Pritchard & Rogers, 2000), with significant implications to upscaling C flux estimates. This prediction, however, has not been tested across soil conditions relevant to models addressing landscape to regional patterns and processes within agroecosystems. Additionally, the relative root productivity responses of annual and perennial herbaceous bioenergy crops to soil properties has not been investigated (Pritchard & Rogers, 2000), limiting our ability to parameterize models focused on understanding impacts of land-use changes from bioenergy production necessary for modeling global C and N cycles. Because these two groups – annual crop and herbaceous perennial species – are adapted to different growth environments, annual and perennial species may have differing strategies for allocating C belowground in heterogeneous environments (Eissenstat & Yanai, 1997), analogous to differences in strategies observed for aboveground productivity. Accurate quantification of such differences in belowground root production is necessary for scaling the effects of bioenergy cropping systems to landscape or regional-scale C cycling models.

At present, estimates of the C cycling impacts from bioenergy are limited by sparse data on soil C inputs from root production. Particularly lacking are side-by-side comparisons of root production from the suite of candidates under consideration for bioenergy crops (US DOE, 2011) and from across environmental gradients representative of the agroecosystems that these crops may be grown within (Cambardella *et al.*, 2004). We developed our study to partially fill this knowledge gap. In this study, we measured the response of root productivity associated with three bioenergy cropping systems arrayed across a topographic gradient with variation in soil conditions representative of the landscape-scale variation commonly found within agroecosystems. Our objective for this study was to evaluate the effect of cropping systems and soil properties on root production, under the assumption that soil properties vary in association with topography. Specifically, we hypothesized that root dynamics would vary by cropping system and landscape position across a hillslope. Alternatively, should landscape position alone not provide sufficient resolution to adequately predict differences in root dynamics, we predicted that variability in root productivity, either within each cropping system or between annual and perennial species, would relate to differences in a suite of soil properties.

Materials and Methods

Site description

This study was conducted as part of the Landscape Biomass Project, located at Iowa State University's Uthe Research and Demonstration Farm in Boone County, Iowa, USA (41°55′N 93°45′W). The experiment consists of a randomized complete block design with five bioenergy cropping systems replicated three times within five blocks. Blocks are located on five landscape positions across a topographic gradient from 325-m to 305-m elevation. Landscape positions were defined along the hillslope according to slope characteristics. Plots measuring 0.05 ha were established in fall 2008 within a 35-ha field previously managed for annual row-crop production according to a corn–soybean rotation for many decades. Portions of plots located on the floodplain position were under perennial vegetation before plot establishment; these portions were delineated before the study and avoided during sampling. Soil series included two Mollisols; Clarion soils are found on all landscape positions except the floodplain, which had Coland series (Table 1). Lesser amounts of Nicolett, Spillville and Zenor soils are also found on site. Mollisols are typical of the temperate humid grasslands native to the mid-latitude region of North America. All soil series have high cation exchange capacity relative to clay content and consist of mixed mineralogy.

Three cropping systems were evaluated in this study, including switchgrass (*Panicum virgatum* L., cv: 'Cave-In-Rock'), continuous corn (*Zea mays* L.), and a triticale/sorghum double crop. The double crop system involves the seeding of a winter annual crop (triticale, × *Triticosecale* Wittm.) in the fall following the harvest of sorghum (*Sorghum bicolor* L. Moench). Nitrogen fertilization was based on nutrient demands of crops and harvest removal rates;

Table 1 Location and description of soil series at the landscape biomass experiment, Boone County, IA, USA (NRCS, 2012)

Soil series	Landscape position[1]	Parent material	Drainage class	Taxonomic class
Clarion	Su, Sh, Bs, Ts	Glacial till	Moderately well-drained	Fine-loamy mesic Typic Hapludolls
Coland	Fp	Alluvium	Poorly drained	Fine-loamy mesic Cumulic Endoaquolls
Nicolett	Su	Glacial till	Somewhat poorly drained	Fine-loamy mesic Aquic Hapludolls
Spillville	Ts	Alluvium	Somewhat poorly drained	Fine-loamy mesic Cumulic Hapludolls
Zenor	Su, Sh	Glacial outwash	Excessively drained	Coarse-loamy mesic Typic Hapludolls

[1] Su, summit; Sh, shoulder; Bs, backslope; Ts, toeslope; Fp, floodplain.

in 2011 corn, sorghum, switchgrass, and triticale were fertilized at a rate of 150, 120, 120 and 30 kg urea-N ha^{-1}, respectively. All plots received 56 kg P_2O_5 ha^{-1} and 112 kg KCl ha^{-1} of Triple Super phosphate, and were managed as no-till. Precipitation for the 2011 growing season from 1 April to 31 October at the site totaled 644 mm, the 20-yr average for the same time period was 662 mm, measured from a long-term climate station located 1.5 km from the research site. Average daily temperatures based on 20 yr for data were within the range observed for the period of the study (Supporting Information Fig. S1).

Root productivity

Annual root production was measured during the 2011 growing season through the use of root ingrowth cores (Steingrobe *et al.*, 2001) to 30-cm soil depth in each plot for the three cropping systems studied. In general, ingrowth methods are thought to be a conservative estimate of root production compared to other methods such as minirhizotron systems and elemental budgets (Hendricks *et al.*, 2006; Milchunas, 2009). Root production estimates can be biased due to proliferation of root growth into root-free soil that may differ chemically and structurally from bulk soil outside of cores, affecting soil moisture or nutrient dynamics (Milchunas, 2009). Additionally, bias may be introduced due to either differential root turnover rates among species or effects on root growth of perennial species (both positive and negative), due to root severing during collection of the initial core. However, ingrowth cores can serve as a useful method for comparison across treatments such as landscape position or heterogeneous edaphic conditions when bias is uniform within a cropping system, (Harmon *et al.*, 2007; Milchunas, 2009).

Ingrowth cores consisted of 64-mm diameter polypropylene mesh tubes (no. 4 mesh) with polypropylene mesh (no. 12 mesh) sown to the tube bottom. Ingrowth core installation involved the collection of a 64-mm diameter soil core to 30 cm depth, sieving (5-mm mesh size) to remove roots, and filling the mesh tube with the root-free soil before placing the ingrowth core into the resulting hole. Three cores per plot were used to estimate root productivity in all annual row-crops (continuous corn, sorghum and triticale). Timing of installation and removal of ingrowth cores within plots was dependent on crop phenology. Ingrowth cores were installed in annual row-crops within 1 wk of seed germination. One core was located within a row for every three cores located between rows to reduce bias of root measurements in row crops (Buczko *et al.*, 2009). Root productivity of the triticale/sorghum cropping system was determined by summing the root production of each crop.

Switchgrass plots were in the third year of production (planted in spring 2009) and were considered near full maturity (Garten *et al.*, 2010); therefore all locations for ingrowth cores were randomly assigned due to the lack of uniform plant spacing. Two sets of three ingrowth cores were installed in each switchgrass plot due to the longer period of growth of the crop and to reduce error in ingrowth estimates from root turnover and decomposition. Switchgrass is harvested following the first hard frost to ensure translocation of N into roots (Wilson *et al.*, 2012); therefore, the first set of cores was deployed in early November 2010 after harvest of the crop. Ingrowth cores were removed during the first week of July 2011, after which the second set was installed in new random locations. The second set of cores was removed within 3 d following harvest of switchgrass during the first week of November 2011. To compare patterns of C allocation, aboveground switchgrass biomass production was determined by clipping plant material within a 1-m^2 quadrat before harvest. Plant material was dried at 65°C and weighed. Additionally, soil cores were collected in switchgrass to estimate the standing crop of root biomass. Three soil cores were randomly collected from within plots with a 32-mm soil probe (Clements Associates, Newton, IA, USA) during the last week of July at the estimated time of maximum standing crop root biomass, based on the timing of switchgrass flowering.

After removal from the field, all ingrowth and standing crop soil cores were stored at 4°C for no > 7 d before processing to isolate root biomass. Soil was washed from roots over 250-µm mesh, and all material remaining on the mesh was dried overnight at 60°C and then stored at room temperature. Sand and debris was hand-sorted from root material in deionized water, and all roots irrespective of root diameter were recovered by filtering cleaned samples through 250-µm mesh. All belowground biomass was recovered from ingrowth cores, including roots and rhizomes. For standing crop soil cores, dead roots and crown nodes (if present) were removed and only live roots and rhizomes were

Table 2 Mean soil parameter values (± SE) across landscape positions

Landscape position	N (g kg^{-1})	SOC (g kg^{-1})	Depth A horizon (cm)	K (ppm)	P (ppm)	Bulk density (g cm^{-3})	GMD	POM (g kg^{-1})	Ksat (cm d^{-1})	Sand (%)	pH
Summit	1.43 (0.23) b	15.8 (1.8) b	33.0 (6.2) b	271 (22.9) a	56.6 (4.2) a	1.58 (0.04) b	0.249 (0.008) c	0.230 (0.017) b	35.0 (3.9) ab	54.1 (5.7) a	6.67 (0.05) a
Shoulder	1.23 (0.07) b	16.6 (0.7) ab	40.2 (3.8) b	202 (18.8) a	33.8 (5.9) a	1.55 (0.03) b	0.239 (0.007) c	0.204 (0.007) b	38.7 (4.5) ab	49.0 (3.1) a	6.60 (0.07) a
Backslope	1.53 (0.15) b	17.9 (1.3) ab	37.8 (6.5) b	157 (34.1) b	13.8 (4.6) b	1.54 (0.05) b	0.262 (0.011) c	0.199 (0.003) b	22.2 (2.9) b	45.5 (1.5) a	6.59 (0.07) a
Toeslope	1.30 (0.14) b	17.8 (1.1) b	46.5 (9.7) b	270 (18.1) a	46.1 (6.2) a	1.58 (0.03) b	0.318 (0.013) b	0.226 (0.018) b	26.1 (3.1) b	52.3 (2.3) a	6.36 (0.19) a
Floodplain	1.93 (0.07) a	31.0 (1.4) a	85.0 (9.8) a	273 (17.1) a	51.0 (5.4) a	1.28 (0.03) a	0.481 (0.042) a	0.345 (0.026) a	48.4 (5.9) a	29.5 (2.6) b	6.65 (0.04) a

Letters indicate significant differences ($P < 0.05$).
Parameter values reported are total soil N content (N), soil organic C content (SOC), soil potassium (K) and phosphorus (P) concentrations, soil bulk density, geometric mean diameter of soil aggregates (GMD), soil particulate organic matter content (POM), saturated hydraulic conductivity of the surface horizon (Ksat), percent sand (sand), and soil pH.

included. Following drying overnight at 60°C, the remaining debris was removed from dried root samples by hand sorting before weighing.

Soil characteristics

Eleven soil properties frequently used as indicators of soil chemical, physical and biological functioning (Doran & Parkin, 1994) were evaluated (Table 2). Eight of the analyses were assessed using samples consisting of five soil cores collected within each plot to 20 cm depth on 28 October 2009 and composited into a single sample. Field-moist samples were sieved with an 8-mm sieve, and half the sample was further passed through a 2-mm sieve. Samples were then air dried at room temperature to a consistent weight. Soil biological characteristics were determined for 8-mm sieved soil, and included soil aggregation and particulate organic matter (POM) content. Aggregates were isolated by wet sieving air-dried soil (Elliot, 1986) and aggregate geometric mean diameter (GMD) was calculated (Kemper & Rosenau, 1986) because aggregate size distributions are generally log-normally distributed (Gardner, 1956). Particulate organic matter (Cambardella & Elliott, 1992) was isolated from aggregate fractions and quantified by loss-on-ignition according to Cambardella *et al.* (2001) and summed to estimate total POM. Soil chemical analyses were performed on the 2-mm sieved soil and included soil organic carbon (SOC), total N, P, K and pH. Soil organic C and total N were measured using a TruSpec Micro CHNS elemental analyzer (LECO Corporation, St Joseph, MI, USA). Soil P and K were measured using Mehlich-3 extractions (Mehlich, 1984) and analyzed using inductively coupled plasma optical emission spectroscopy (IRIS Intrepid ICP-OES; Thermo Scientific, Pittsburgh, PA, USA). Soil pH (Thomas, 1996) was measured on 1 : 1 deionized water : soil slurries from 50-g subsamples (Orion PerpHect 320; Thermo Scientific). Soil physical characteristics included determination of particle size distribution, bulk density, saturated hydraulic conductivity and measurement of the depth of the A horizon. Soil sand percentage was determined from particle size analysis on 2-mm sieved soil (10-g subsamples) using the pipette method (Kettler *et al.*, 2001). Bulk density was measured using oven-dried soil mass and the sample field volume (Blake & Hartge, 1986) averaged from three samples per plot. Within each plot, saturated hydraulic conductivity was measured ($n = 3$) in the top 10 cm of soil using a permeameter (Precision Permeameter; Johnson Permeameter LLC, Fairfax, VA, USA) to estimate water infiltration rates. Average depth of the soil A horizon was determined from two 5-cm diameter soil cores collected to 120-cm depth in each plot using a Giddings Soil Probe (#15 Series; Giddings Machine Company, Windsor, CO, USA). Soil cores were described according to Schoeneberger *et al.* (2002), including delineation of soil horizons.

Statistical analyses

Data were transformed to meet assumptions of normality when necessary. Root production and above- and belowground biomass were analyzed using mixed-model analysis of variance

(ANOVA), with either cropping system or landscape position as fixed effects and replicates treated as a random effect. Comparisons of means were analyzed with Tukey HSD *post-hoc* tests. ANOVA analyses were performed using SAS statistical software (SAS v9.3; SAS Institute Inc., Cary, NC, USA). Dissimilarity analysis of soil quality variables among landscape positions was performed using Multiple Response Permutation Procedure (MRPP) analysis with euclidean distances in the Vegan package (Oksanen *et al.*, 2012) in R v2.15.1 (R Core Team, 2012). Due to significant collinearity among soil parameters, soil variables used for multiple linear regression analyses were determined using maximum likelihood exploratory factor analysis with VARIMAX rotation in R. The optimal number of factors chosen was determined using parallel analysis in the nFactor package (Raiche & Magis, 2010). For each factor chosen, one variable is selected with the highest loading to represent that individual factor to establish a reduced variable set (Dormann *et al.*, 2012). Multiple linear regression was used for predicting root productivity from soil quality variables, using the best subsets selection criteria based on Aikaike's Information Criterion adjusted for small sample sizes (AIC$_c$) using SAS statistical software. Condition index was used as a diagnostic measure to quantify the severity of collinearity of selected models, with threshold values of > 30 indicating critical severity of collinearity (Belsley *et al.*, 1980). Model parameters were considered significant at $P < 0.05$.

Results

Cropping system and topographic effects

Annual root production was significantly different among all three cropping systems ($F = 37.2$, $P < 0.0001$), suggesting that bioenergy cropping system can serve as a good predictor for scaling estimates of root production to landscapes. Averaged across landscape positions, switchgrass had significantly higher root production (280 g m^{-2}) than either of the annual cropping systems, producing twice as much root biomass as the continuous corn system. Additionally, triticale/sorghum had significantly greater root productivity at 171 g m^{-2} compared to 139 g m^{-2} for continuous corn.

Landscape position was generally a poor predictor of root productivity. Although not significant at the $P = 0.05$ level, root production averaged across all cropping systems showed a trend towards being influenced by landscape position ($F = 2.33$, $P = 0.061$), largely due to the influence of the switchgrass cropping system. For the annual cropping systems, variability of root production was high within landscape positions (Fig. 1); therefore, we were unable to detect any significant effects of landscape position ($F = 0.29$, $P = 0.882$, corn; $F = 0.26$, $P = 0.90$, triticale/sorghum). For the perennial switchgrass system, landscape position did not impact aboveground biomass ($F = 2.47$, $P = 0.112$, data not shown), but did significantly influence annual root production ($F = 4.56$, $P = 0.004$; Table 3) due to lower productivity on the floodplain position (Fig. 1). The highest productivity was observed on the toeslope, summit and shoulder, which averaged 43% greater root production than the floodplain. Mean root productivity on the backslope position was lower than observed on the summit, shoulder and toeslope; however, these differences were not significant due to the high variability of the data and low sample size, which may have increased the chances of type II errors. Additionally, regression analysis showed that the aboveground biomass of switchgrass was not significantly correlated to root production ($F = 0.01$, $P = 0.449$, data not shown), suggesting that reductions in root production in the floodplain were not coincident with a decrease in aboveground primary production, but rather a decrease in C allocation to belowground productivity. Likewise, the standing crop root biomass of switchgrass did not differ across the toposequence after adjusting for multiple comparisons (Table 4), although before adjustment the overall test indicated root biomass was lower in the toeslope and floodplain relative to the summit and shoulder ($F = 2.89$, $P = 0.036$).

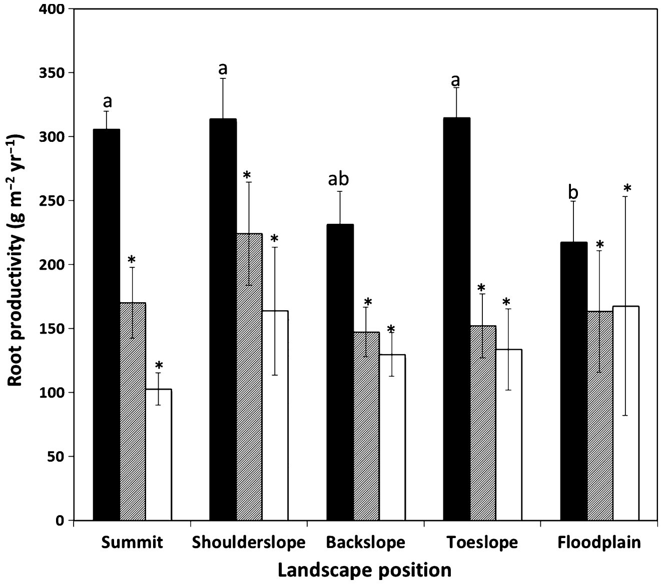

Fig. 1 Mean root production for cropping systems among landscape positions. Switchgrass, black bars; triticale/sorghum, grey bars; continuous corn, white bars. Letters indicate significant differences ($P < 0.05$) across landscape positions within a cropping system. Error bars show + 1 SE; *, no significant differences among landscape positions within a cropping system.

Table 3 *P*-values for pairwise comparisons of root production estimates among different landscape positions for the switchgrass cropping system

Landscape position				
	Shoulder	Backslope	Toeslope	Floodplain
Summit	0.906	0.590	0.964	0.011
Shoulder		0.665	0.999	0.015
Backslope			0.569	0.286
Toeslope				0.009

Multiple response permutation procedure analysis indicated a significant difference among landscape positions based on analysis of all 11 soil parameters. Differences determined through estimation of the chance-corrected within-group agreement – which describes the within-group homogeneity compared to the

Table 4 Mean standing crop root biomass (± SE) of switchgrass across landscape positions

Landscape position	Root biomass (g m^{-2})
Summit	639.1 (67.3) a
Shoulder	628.9 (72.7) a
Backslope	490.4 (46.8) a
Toeslope	432.8 (33.3) a
Floodplain	456.8 (61.3) a

Letters indicate significant differences ($P < 0.05$).

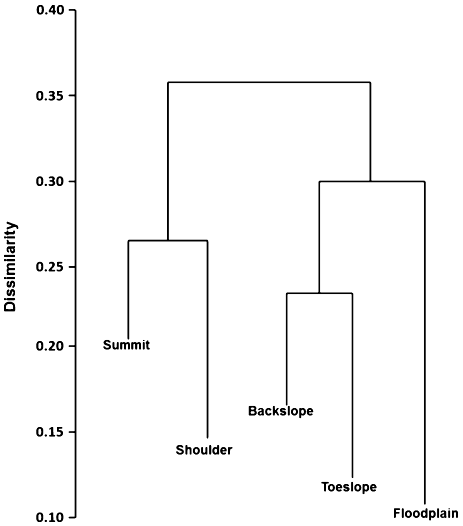

Fig. 2 Mean dissimilarity dendrogram showing relationships among landscape positions based on within- and between-group dissimilarities of mean distances among 11 soil parameters included in the analyses. Horizontal lines are drawn at the levels of mean between-cluster dissimilarity, vertical lines hang to levels of within-cluster dissimilarity.

random expectation – were significant ($A = 0.135$, $P < 0.001$). Dissimilarity among landscape positions was larger than within-group dissimilarity among all groups (Fig. 2), suggesting that landscape positions were distinct from one another according to the soil parameters used in this study (Table 2). For example, backslope and toeslope were the most similar among all the landscape positions, yet the within-group dissimilarity for both these positions was lower than their between-group dissimilarity, indicating that these positions were distinct from one another. Results show that floodplain soils were the most distinct from other landscape positions, while having the highest within-group similarity. Soils on the summit, the only position consisting of three separate soil series (Table 1), showed the highest amount of within-group dissimilarity, yet this dissimilarity was still lower than among the most similar positions. Dissimilarity among landscape positions was due to differences observed in the individual soil characteristics which varied across landscape positions for all but one parameter (Table 2). Floodplain soils had the most differences relative to other positions, with higher SOC, total N, A horizon depth, GMD and POM, and lower soil sand percentage and bulk density compared to other locations. Backslope soils showed lower P and K content compared to other landscape positions, while saturated hydraulic conductivity was lower in the backslope and toeslope soils compared to the floodplain.

Identifying predictors of root production

Multiple linear regression before reduction of the set of explanatory variables indicated significant collinearity among predictor variables (Table S1), with condition index values of regression models greater than the threshold value of 30 (Dormann *et al.*, 2012). Under these conditions, the estimation equation for the regression parameters is ill-conditioned, resulting in parameter estimates that are unstable due to inflated standard errors. Maximum likelihood factor analysis was used to partition variables into subsets to reduce the number of predictors to eliminate collinearity of variables for model selection (Comrey & Lee, 1992). Four factors were found to be optimal based on parallel analysis (Franklin *et al.*, 1995), comprising 69% of the total variation within the soil characteristics. The most important factor accounted for 30% of the variation and represented the soil physical characteristics, with percent sand having the highest loading (0.92). The second factor accounted for an additional 16% of the variation, and largely described the soil mineral nutrient content with P and K showing the highest loading (0.94 and 0.69, respectively). Variables related to SOM content (GMD and POM; loadings 0.89 and 0.40, respectively) comprised the third factor, explaining an additional 12% of the variation. Finally, the fourth factor was represented solely by saturated hydraulic conductivity (0.97), constituting an additional 11% of the variation.

Factor analysis identified a reduced set of variables for evaluating root productivity, including percent sand, P, GMD and saturated hydraulic conductivity. Multiple linear regression analysis across all cropping systems showed percent sand was the only significant variable ($F = 6.61$, $P = 0.014$) affecting root production, explaining 11% of the variation in the root production data, largely due to the influence of switchgrass. Within cropping systems, percent sand was the only significant predictor for switchgrass root productivity ($F = 11.78$, $P = 0.004$), accounting for 45% of the variability of the data (Fig. 3), and no model was significant for root productivity of either corn or triticale/sorghum cropping systems. Additional regression on individual soil parameters show switchgrass root production was negatively correlated with SOC ($F = 8.71$, $P = 0.011$, adjusted $R^2 = 0.355$) and total N ($F = 6.85$, $P = 0.021$, adjusted $R^2 = 0.295$) contents, and positively correlated with bulk density ($F = 5.04$, $P = 0.043$, adjusted $R^2 = 0.224$; Fig. 3).

Our results do not lend strong support for the hypothesis that landscape position is a useful predictor of root productivity. Additionally, our alternative hypothesis that variability in root production is related to differences in soil properties was not substantiated in the annual cropping systems. However, our results for the switchgrass cropping system do support our alternative hypothesis that root production may be predicted based on differences in edaphic characteristics. Furthermore, our results suggest that percent sand, an easily measured soil property, may serve as a proxy for other important soil variables.

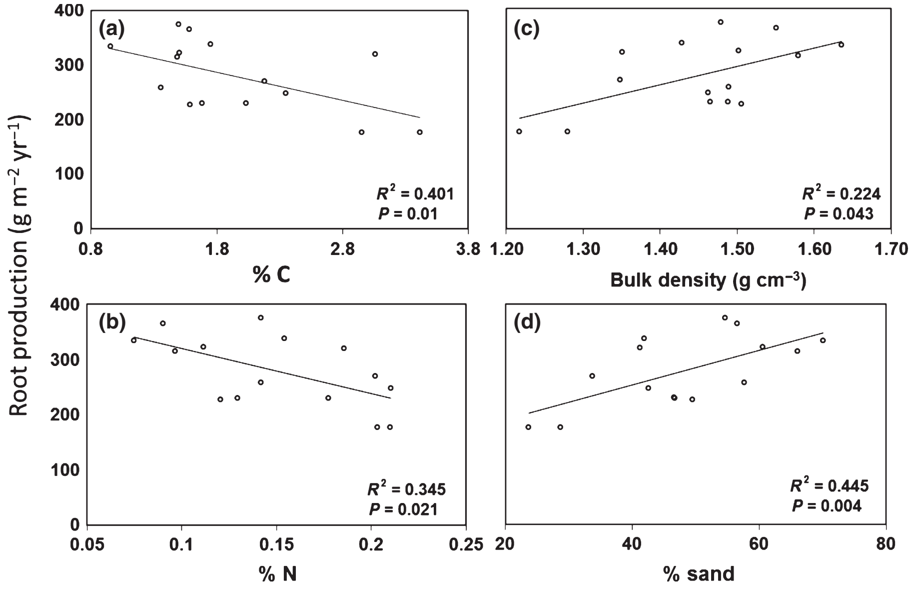

Fig. 3 Root productivity in switchgrass as a function of (a) soil organic carbon content (SOC) content, (b) total nitrogen (N) content, (c) bulk density, (d) percentage sand.

Discussion

Environmental heterogeneity often affects drivers of biogeochemical processes, which are typically multivariate, influencing pools and fluxes of nutrients across landscapes (Turner, 2005). Scaling measurements of complex ecosystems is challenging, requiring the reduction of system complexity on the basis of experimental evidence to deduce key drivers of processes (Wagenet, 1998; Osmond *et al.*, 2004). We provide evidence that annual and perennial bioenergy cropping systems differ in root productivity, and that heterogeneous edaphic conditions impact root production of cropping systems differently. Our findings address the need for empirical data on variability of bioenergy crop root production within agroecosystems, necessary for predicting the influence of bioenergy production on C cycling dynamics.

Root productivity of cropping systems

We observed differences in root production among all cropping systems indicating that bioenergy crop serves as a strong predictor of root productivity. Our results were consistent with expectations of relative differences in root production among annual and perennial crops (Schroetter *et al.*, 2005; Anderson-Teixeira *et al.*, 2013). Although biases introduced by ingrowth methodology may make accurate comparisons across sites and among species difficult, root production was generally consistent with data reported elsewhere: corn root productivity was within the range reported by Russell *et al.* (2009) in Iowa, while belowground production of switchgrass in our study was 13% lower than similarly aged switchgrass stands in Tennessee, USA, determined by sequential coring (Garten *et al.*, 2010). Although no studies were found comparing production rates of the triticale/sorghum double crop due to the novelty of this cropping system, root production was lower than the 220 g m^{-2} in sorghum reported by Cheng *et al.* (1990) on Georgia Piedmont soils.

Our findings provide strong empirical evidence that the provisioning of environmental benefits derived from bioenergy will in part be dependent on the relative use of annual or perennial species across landscapes (Robertson *et al.*, 2011). High root productivity is critical for optimal root:shoot partitioning, a key trait of bioenergy crops necessary for sustainable yields (Karp & Shield, 2008). Boosting belowground productivity is critical for increased soil C storage potential of agroecosystems (Ma *et al.*, 2000; Sartori *et al.*, 2006), a critical component of ecosystem function relative to greenhouse gas emissions (Anderson-Teixeira & DeLucia, 2011). Our results support other studies that suggest maximizing the environmental benefits of belowground C cycling from bioenergy require using perennial feedstocks such as switchgrass (Anderson-Teixeira *et al.*, 2013).

Topographic and edaphic impacts on root productivity

Landscape position classification based on terrain attributes can aid in determining locations where variation is important for scaling key ecosystem processes. Analysis of soil characteristics has been used as an indicator of landscape position differences in soil conditions (Ovalles & Collins, 1986). We found landscape positions were distinct, suggesting that the edaphic conditions roots were exposed to differ along the toposequence. Compared across the toposequence, variability of soil parameters within landscape positions was significantly less than among positions (Fig. 3). The effects of topography on soil properties are well documented, with typically strong relationships between topography and both SOC and N at field scales (Schimel *et al.*, 1985; Wood *et al.*, 1990; Senthilkumar *et al.*, 2009), largely due to soil redistribution (Pennock *et al.*, 1994). Similar to these studies, soil parameter patterns at our site showed higher SOC, total N, soil aggregation and POM in the floodplain, along with decreased bulk density and percent sand. Erosion changes A-horizon thickness (Pennock *et al.*, 1994) and results in the loss of fine soil particles, especially clays (Lance *et al.*, 1986). Our data show infiltration rates and soil P and K content were lower in sloped areas of the toposequence, similar to previous studies (Gburek & Sharpley, 1998; Elliot & Efetha, 1999).

Effective modeling of nutrient cycles across landscapes requires empirical data on spatial variation in root responses (Pritchard & Rogers, 2000); considering societal expectations for the sustainability of bioenergy, species-specific responses may be particularly important. We hypothesized that root productivity of bioenergy cropping systems would show differences across the toposequence from the distinct edaphic conditions associated with landscape position. Contrary to our expectations, landscape position did not affect root production in either corn or triticale/sorghum cropping system. High variability of root production may partly be due to patchy distribution of annual row crop rhizospheres (Buczko *et al.*, 2009), making detection of differences across the toposequence more challenging than in perennial systems. Switchgrass root production in our study was lower in the floodplain than in other landscape positions (summit, shoulder and toeslope). Switchgrass aboveground biomass did not change across landscape positions and was not correlated with root production (data not shown), suggesting that changes in root production on the floodplain were not due to a decrease in overall productivity, but instead to decreased C allocation to roots.

Root productivity has been shown to respond either positively to nutrient concentrations (Drew, 1975), or to decrease (Hunt & Burnett, 1973) as predicted by optimal partitioning theory (Bloom *et al.*, 1985); patterns of this response vary among species (McCarthy & Enquist, 2007). Our results show that switchgrass root production decreased in the floodplain where nutrient conditions were highest, but we did not detect the corresponding increase in aboveground production predicted by optimum partitioning theory. Nadelhoffer (2000) proposed that decreasing C allocation to roots with increasing soil nutrients could result from root turnover rates either remaining constant or decreasing. We found no differences in standing crop root biomass of switchgrass across landscape positions (Table 4), suggesting that root turnover may be either remaining constant or decreasing with higher nutrient contents (Nadelhoffer, 2000). Thus, while root turnover was not assessed in this study, different root turnover rates could explain lower C allocation to roots in switchgrass with increasing soil N in the floodplain. Our results suggest that realized impacts to belowground C storage from switchgrass grown for bioenergy might be lower in certain portions of the landscape, such as floodplain sites; models based only on C inputs from upland locations may overestimate C storage potential.

In the two annual cropping systems evaluated in this study, soil parameters were not significant predictors of root production. Management impacts can significantly affect root production of corn, typically through tillage and crop residue management practices that impact soil physical properties such as bulk density, soil moisture and SOM (Barber, 1970). Our results indicate that either root production in annual crops does not respond to soil conditions at the scale measured, or root production is affected by variables not quantified in this study.

Due to the influence of SOM contents on many physical, chemical and biological properties of soil, edaphic factors are often correlated to some extent. For example, SOC content is correlated with high clay contents (Burke *et al.*, 1989) and increased soil aggregation, often leading to higher N and P concentrations (Elliot, 1986). Our data show similar patterns (Table S1), necessitating a reduced soil parameter data set to model root production. Multiple linear regression analysis revealed that percent sand was the single significant parameter for predicting switchgrass root productivity. However, linear regressions with individual soil parameters showed that switchgrass root production was also positively correlated with bulk density and negatively associated with indicators of increased soil nutrient content (total N and SOC; Fig. 3). These results support the expectations of a reduced root productivity response to increasing nutrient supply based on optimum partitioning theory (Bloom *et al.*, 1985) and cost–benefit theory (Eissenstat & Yanai, 1997).

Upscaling root production based on topographic and edaphic conditions

Linking environmental heterogeneity to ecosystem processes can provide a powerful tool for scaling estimates of ecosystem processes (Turner, 2005). However, there is surprisingly little research addressing root production across heterogeneous conditions necessary for scaling measurements to fields, landscapes and beyond. Our study is the first we are aware of providing empirical data on the spatial variation of perennial herbaceous species or contrasting annual and perennial species essential for predicting root production in bioenergy crops across intermediate scales (10–1000s m^2).

A patch-based spatial scaling approach assumes that the functionality of landscapes is the sum of its component patches (Wu & Levin, 1997), which can be appropriate for extrapolating processes based on vegetation and soil characteristics (Zhang *et al.*, 2007). Similarly, root production can be linked to patch-based units, such as landscape position, which may be useful for scaling purposes. Our results suggest that using a patch-based approach has limited usefulness for scaling plot-level measurements of root production of switchgrass by stratifying landscapes using terrain attributes and soil maps; such an approach will not work for annual crops. Relationships between landscape position and switchgrass root productivity can be used to extrapolate root productivity estimates to regional scales based on the aerial extent of floodplain and upland soils (sensu Groffman *et al.*, 1992).

Scaling estimates of root production using continuous variation in soil parameters have advantages over patch-based scaling approaches. Many continuous variables are easily measured or widely available at high resolutions through soil geodatabases, especially in agricultural regions expected to be impacted by bioenergy. As we have shown, landscape positions may correlate well with soil parameters such as sand content, bulk density, and SOC and N concentrations. The DAYCENT model has recently been used to predict the impacts of bioenergy production on C and greenhouse gas fluxes at regional scales (Davis *et al.*, 2012), but currently does not incorporate spatial variation in soil parameters such as texture in the plant growth sub-model that determines root C inputs (Del Grosso *et al.*, 2001). Regression equations can be integrated into C cycling models (Burke *et al.*, 1990) that predict spatial variation of root production using existing spatially explicit soil databases. The impact will be improved model predictions and understanding of the uncertainty therein (Harmon *et al.*, 2007; Lehrter & Cebrian, 2010; Yanai *et al.*, 2010).

Conclusions

Accuracy in scaling up measurements of ecosystem processes requires linking spatial heterogeneity in critical drivers to the variation in responses. Our study addresses the need to provide empirical data on the root production of bioenergy crops across variable topographic and edaphic conditions common within agroecosystems. Our results show that root production varied among cropping systems, suggesting that cropping system can be used as a good predictor over broader spatial scales and that impacts to belowground C cycling will be dependent on crop type (Sartori *et al.*, 2006; Anderson-Teixeira *et al.*, 2013). While root productivity of annual bioenergy cropping systems was not affected by landscape position, root production in switchgrass was lower in the floodplain location, suggesting that landscape position has some limited predictive value.

Root production within annual cropping systems was highly variable and could not be predicted using edaphic factors. However, switchgrass root production was best predicted with the sand percentage across our site, but also responded positively to bulk density and negatively to soil C and N content. Widely available variables such as soil texture delineated in geospatial soil databases may aid in predicting root productivity of perennial bioenergy crops for scaling estimates of C and N cycling to landscapes and beyond. Our results indicate that the realized environmental benefits of land-cover conversion to bioenergy switchgrass may differ based on variation in soil properties. Margin lands not well suited for annual crop production may be critical for bioenergy to be sustainable (Gelfand *et al.*, 2013). Our results further suggest that switchgrass grown on sites with sandy soils and low nutrient content may have enhanced C inputs from root production relative to more productive soils. Future work is needed to test the extent to which these findings are more broadly representative of annual and perennial bioenergy cropping systems.

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References

Anderson-Teixeira KJ, DeLucia EH. 2011. The greenhouse gas value of ecosystems. *Global Change Biology* **17**: 425–438.

Anderson-Teixeira KJ, Masters MD, Black CK, Zeri M, Hussain MZ, Bernacchi CJ, DeLucia EH. 2013. Altered belowground carbon cycling following land-use change to perennial bioenergy crops. *Ecosystems.* doi: 10.1007/s10021-012-9628-x.

Barber SA. 1970. Effect of tillage practices on corn (*Zea mays* L.) root distribution and morphology. *Agronomy Journal* **63**: 724–726.

Belsley DA, Kuh E, Welsch RE. 1980. *Regression diagnostics: identifying influential data and sources of collinearity.* New York, NY, USA: John Wiley & Sons.

Blake GR, Hartge KH. 1986. Bulk density. In: Klute A, ed. *Methods of soil analysis. Part 1. Physical and mineralogical methods, 2nd edn.* Madison, WI, USA: American Society of Agronomy and Soil Science Society of America, 363–376.

Bloom AJ, Chapin FS, Mooney HA. 1985. Resource limitation in plants – an economic analogy. *Annual Review of Ecology & Systematics* **16**: 363–392.

Buczko U, Kuchenbuch RO, Gerke HH. 2009. Evaluation of a core sampling scheme to characterize root length density in maize. *Plant and Soil* **315**: 297–314.

Burke IC, Schimel DS, Yonkers CS, Parton WJ, Joyce LA, Lauenroth WK. 1990. Regional modeling of grassland biogeochemistry using GIS. *Landscape Ecology* **4**: 45–54.

Burke IC, Yonker CM, Parton WJ, Cole CV, Schimel DS, Flach K. 1989. Texture, climate, and cultivation effects on soil organic matter content in US grassland soils. *Soil Science Society of America Journal* **53**: 800–805.

Cambardella CA, Elliott ET. 1992. Carbon and nitrogen changes across a grassland cultivation sequence. *Soil Science Society of America Journal* **56**: 777–783.

Cambardella CA, Gajda AM, Doran JW, Wienhold BJ, Kettler TA. 2001. Estimation of particulate and total organic matter by weight loss-on-ignition. In: Lal R, Kimble JM, Follett RF, Stewart BA, eds. *Assessment methods for soil carbon.* Boca Raton, FL, USA: CRC Press, 349–359.

Cambardella CA, Moorman TB, Andrews SS, Karlen DL. 2004. Watershed-scale assessment of soil quality in the loess hills of southwest Iowa. *Soil & Tillage Research* **78**: 237–247.

Cambardella CA, Moorman TB, Novak JM, Parkin TB, Karlen DL, Turco RF, Konopka AE. 1994. Field-scale variability of soil properties in central Iowa soils. *Soil Science Society of America Journal* **58**: 1501–1511.

Cheng W, Coleman DC, Box JE. 1990. Root dynamics, production and distribution on the Georgia Piedmont using minirhizotrons. *Journal of Applied Ecology* **27**: 592–604.

Comrey AL, Lee HB. 1992. *A first course in factor analysis, 2nd edn.* Hillsdale, NJ, USA: Lawrence Erlbaum Associates.

Dale VH, Kline KL, Wright LL, Perlack RD, Downing M, Graham RL. 2011. Interactions among bioenergy feedstock choices, landscape dynamics, and land use. *Ecological Applications* **21**: 1039–1054.

Davis SC, Parton WJ, Del Grosso SJ, Keough C, Marx E, Adler P, DeLucia EH. 2012. Impacts of second-generation biofuel agriculture on greenhouse gas emissions in the corn-growing regions of the US. *Frontiers in Ecology and the Environment* **10**: 69–74.

Del Grosso SJ, Parton WJ, Mosier AR, Hartman MD, Brenner J, Ojima DS, Schimel DS. 2001. Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model. In: Schaffer MJ, Ma L, Hansen S, eds. *Modeling carbon and nitrogen dynamics for soil management.* Boca Raton, FL, USA: CRC Press, 303–331.

Dexter AR. 2004. Soil physical quality Part I. Theory, effects of soil texture, density, and organic matter, and effects on root growth. *Geoderma* **120**: 201–214.

Doran JW, Parkin TB. 1994. Defining and assessing soil quality. In: Doran JW, Coleman DC, Bezdicek DF, Stewart BA, eds. *Defining soil quality for a sustainable environment.* Madison, WI, USA: American Society of Agronomy, 3–22.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marquéz JR, Gruber B, Lafourcade B, Leitão PJ *et al.* 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **35**: 1–20.

Drew MC. 1975. Comparison of the effects of a localized supply of phosphate, nitrate, ammonium, potassium on the growth of the seminal root system, and the shoot, in barley. *New Phytologist* **75**: 479–490.

Eissenstat DM, Yanai RD. 1997. The ecology of root lifespan. *Advances in Ecological Research* **27**: 1–60.

Elliot ET. 1986. Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. *Soil Science Society of America Journal* **50**: 627–633.

Elliot JA, Efetha AA. 1999. Influence of tillage and cropping system on soil organic matter, structure and infiltration in a rolling landscape. *Canadian Journal of Soil Science* **79**: 457–463.

Fitter AH. 1987. An architectural approach to the comparative ecology of plant-root systems. *New Phytologist* **106**: 61–77.

Franklin JF. 2005. Spatial pattern and ecosystem function: reflections on current knowledge and future directions. In: Lovett GM, Jones CG, Turner MG, Weathers KC, eds. *Ecosystem function in heterogeneous landscapes.* New York, NY, USA: Springer, 427–441.

Franklin SB, Gibson DJ, Robertson PA, Pohlmann JT, Fralish JS. 1995. Parallel analysis: a method for determining significant principal components. *Journal of Vegetation Science* **6**: 99–106.

Gardner WR. 1956. Representation of soil aggregate-size distribution by a logarithmic-normal distribution. *Science Society of America Journal* **20**: 151–153.

Garten CT, Kang S, Brice DJ, Schadt CW, Zhou J. 2007. Variability in soil properties at different spatial scales (1 m–1 km) in a deciduous forest system. *Soil Biology & Biochemistry* **39**: 2621–2627.

Garten CT, Smith JL, Tyler DD, Amonette JE, Bailey VL, Brice DJ, Castro HF, Graham RL, Gunderson CA, Izaurralde RC *et al.* 2010. Intra-annual changes in biomass, carbon and nitrogen dynamics at 4-year old switchgrass field trials in west Tennessee, USA. *Agriculture, Ecosystems and Environment* **136**: 177–184.

Gburek WJ, Sharpley AN. 1998. Hydrologic controls on phosphorus loss from upland agricultural watersheds. *Journal of Environmental Quality* **27**: 267–277.

Gelfand I, Sahajpal S, Zhang X, Izaurralde RC, Gross KL, Robertson GP. 2013. Sustainable bioenergy production from marginal lands in the US Midwest. *Nature* **493**: 514–517.

Gill RA, Kelly RH, Parton WJ, Day KA, Jackson RB, Morgan JA, Scurlock JMO, Tieszen LL, Castle JV, Ojima DS *et al.* 2002. Using simple environmental variables to estimate belowground productivity in grasslands. *Global Ecology & Biogeography* **11**: 79–86.

Groffman PM, Tiedje JM, Mokma DL, Simkins S. 1992. Regional scale analysis of denitrification in northern temperate forest soils. *Landscape Ecology* **7**: 45–53.

Harmon ME, Phillips DL, Battles JJ, Rassweiler A, Hall RO, Lauenroth WK. 2007. Quantifying uncertainty in net primary production measurements. In: Fahey TJ, Knapp AK, eds. *Principles and standards for measuring primary production.* New York, NY, USA: Oxford University Press, 238–262.

Hendricks JJ, Hendrick RL, Wilson CA, Mitchell RJ, Pecot SD, Guo D. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology* **94**: 40–57.

Hodge A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9–24.

Hunt R, Burnett JA. 1973. The effects of light intensity and external potassium concentration on root/shoot ratio and rates of potassium uptake in perennial ryegrass (*Lolium perenne* L.). *Annals of Botany* **37**: 519–537.

Jagadamma S, Lal R, Rimal BK. 2009. Effects of topsoil depth and soil amendments on corn yield and properties of two Alfisols in central Ohio. *Journal of Soil Water Conservation* **64**: 70–80.

Jones CA. 1983. Effect of soil texture on critical bulk densities for root growth. *Soil Science Society of America Journal* **47**: 1208–1211.

Jordan N, Boody G, Broussard W, Glover JD, Keeney D, McCown BH, McIsaac G, Muller M, Murray H, Neal J *et al.* 2007. Sustainable development of the agricultural bio-economy. *Science* **306**: 1570–1571.

Karp A, Shield I. 2008. Bioenergy from plants and the sustainable yield challenge. *New Phytologist* **179**: 15–32.

Kemper WD, Rosenau RC. 1986. Aggregate stability and size distribution. In: Klute A, ed. *Methods of soil analysis. Part 1. Physical and mineralogical methods. 2^{nd} edn.* Madison, WI, USA: American Society of Agronomy, 425–442.

Kettler TA, Doran JW, Gilbert TL. 2001. Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Science Society of America Journal* **65**: 849–852.

Lance JC, McIntyre SC, Naney JW, Rousseva SS. 1986. Measuring sediment movement at low erosion rates using cesium-137. *Soil Science Society of America Journal* **50**: 1303–1309.

Lehrter JC, Cebrian J. 2010. Uncertainty propagation in an ecosystem nutrient budget. *Ecological Applications* **20**: 508–524.

Ma Z, Wood CW, Bransby DI. 2000. Soil management impacts on soil carbon sequestration by switchgrass. *Biomass and Bioenergy* **18**: 469–477.

McCarthy MC, Enquist BJ. 2007. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology* **21**: 713–720.

Mehlich A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. *Communications in Soil Science and Plant Analysis* **15**: 1409–1416.

Milchunas DG. 2009. Estimating root production: comparison of 11 methods in shortgrass steppe and review of biases. *Ecosystems* **12**: 1381–1402.

Nadelhoffer KJ. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytologist* **147**: 131–139.

Natural Resources Conservation Service (NRCS), United States Department of Agriculture. 2012. *Soil survey geographic (SSURGO) database for boone county, IA, USA.* [WWW document] URL: http://soildatamart.nrcs.usda.gov [accessed 20 November 2009].

Oksanen JF, Blanchet G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Wagner H. 2012. *vegan: community ecology package.* R package version 2.0-5. [WWW document] URL: http://CRAN.R-project.org/package=vegan [accessed 1 September 2012].

Osmond B, Ananyev G, Berry J, Langdon C, Kolber Z, Gunghui L, Monson R, Nichol C, Rascher U, Schurr U *et al.* 2004. Changing the way we think about global research: scaling up in experimental ecosystem science. *Global Change Biology* **10**: 393–407.

Ovalles FA, Collins ME. 1986. Soil–landscape relationships and soil variability in North Central Florida. *Soil Science Society of America Journal* **50**: 401–408.

Pennock DJ, Anderson DW, de Jong E. 1994. Landscape scale changes in indicators of soil quality due to cultivation in Saskatchewan, Canada. *Geoderma* **64**: 1–19.

Peters DPC, Bestelmeyer BT, Turner MG. 2007. Cross–scale interactions and changing pattern–process relationships: consequences for system dynamics. *Ecosystems* **10**: 790–796.

Pritchard SG, Rogers HH. 2000. Spatial and temporal deployment of crop roots in CO_2-enriched environments. *New Phytologist* **147**: 55–71.

R Core Team. 2012. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. [WWW document] URL: http://www.R-project.org [accessed 24 August 2012].

Raiche G, Magis DM. 2010. *Parallel analysis and non-graphical solutions to the cattell scree test.* R package version 2.3.3. [WWW document] URL: http://cran.r-project.org/web/packages/nFactors [accessed 1 September 2012].

Robertson GP, Hamilton SK, Del Grosso SJ, Parton WJ. 2011. The biogeochemistry of bioenergy landscapes: carbon, nitrogen, and water considerations. *Ecological Applications* **21**: 1055–1067.

Russell AE, Cambardella CA, Laird DA, Jaynes DB, Meek DW. 2009. Nitrogen fertilizer effects on soil carbon balances in Midwestern US agricultural systems. *Ecological Applications* **19**: 1102–1113.

Sartori F, Lal R, Ebinger MH, Parrish DJ. 2006. Potential soil carbon sequestration and CO_2 offset by dedicated energy crops in the USA. *Critical Reviews in Plant Sciences* **25**: 441–472.

Schimel DS, Coleman DC, Horton KA. 1985. Soil organic matter dynamics in a paired rangeland and cropland toposequences in North Dakota. *Geoderma* **36**: 201–214.

Schoeneberger PJ, Wysocki DA, Benham EC, Broderson WD. 2002. *Field book for describing and sampling soils, version 2.0.* Lincoln, NE, USA: Natural Resource Conservation Service, National Soil Survey Center.

Schroetter S, Schnug E, Rosasik J. 2005. Root growth and agricultural management. In: Lal R, ed. *Encyclopedia of soil science, 2^{nd} edn.* Boca Raton, FL, USA: CRC Press, 1531–1547.

Senthilkumar S, Kravchenko AN, Robertson GP. 2009. Topography influences management system effects on total soil carbon and nitrogen. *Soil Science Society of America Journal* 73: 2059–2067.

Steingrobe BE, Schmid H, Claassen N. 2001. The use of the ingrowth core method for measuring root production of arable crops – influence of soil and root disturbance during installation of the bags on root ingrowth into the cores. *European Journal of Agronomy* 15: 143–151.

Stott DE, Cambardella CA, Tomer MD, Karlen DL, Wolf R. 2011. A soil quality assessment within the Iowa River South Fork watershed. *Soil Science Society of America Journal* 75: 2271–2282.

Taubert F, Frank K, Huth A. 2012. A review of grassland models in the biofuel context. *Ecological Modelling* 245: 84–93.

Thomas GW. 1996. Soil pH and acidity. In: Sparks DL, ed. *Methods of soil analysis. Part 3 – chemical methods.* Madison, WI, USA: American Society of Agronomy/ Soil Science Society of America, 475–490.

Turner ME. 2005. Landscape ecology in North America: past, present, and future. *Ecology* 86: 1967–1974.

Unger PW, Kaspar TC. 1994. Soil compaction and root growth – a review. *Agronomy Journal* 86: 759–766.

US Department of Energy (DOE). 2011. *U.S. billion-ton update: biomass supply for a bioenergy and bioproducts industry.* Perlack RD, Stokes BJ, study leads. ORNL/TM-2011/224. Oak Ridge, TN, USA: Oak Ridge National Laboratory.

Wagenet RJ. 1998. Scale issues in agroecological research chains. *Nutrient Cycling in Agroecosystems* 50: 23–34.

Wilson DM, Dalluge DL, Rover M, Heaton EA, Brown RC. 2012. Crop management impacts biofuel quality: influence of switchgrass harvest time on yield, nitrogen and ash of fast pyrolysis products. *Bioenergy Research* 5: 86–94.

Wood CW, Westfall DG, Peterson GA, Burke IC. 1990. Impacts of cropping intensity on carbon and nitrogen mineralization under no-till dryland agroecosystems. *Agronomy Journal* 82: 1115–1120.

Wu J, Levin SA. 1997. A patch-based spatial modeling approach: conceptual framework and simulation scheme. *Ecological Modelling* 101: 325–346.

Yanai RD, Battles JJ, Richardson AD, Blodgett CA, Wood DM, Rastetter EB. 2010. Estimating uncertainty in ecosystem budget calculations. *Ecosystems* 13: 239–248.

Yuan ZY, Chen HY. 2012. A global analysis of fine root production as affected by soil nitrogen and phosphorus. *Proceedings of the Royal Society B* 279: 3796–3802.

Zhang N, Zhenliang Y, Guirui Y, Wu J. 2007. Scaling up ecosystem productivity from patch to landscape: a case study of Changbai Mountain Reserve, China. *Landscape Ecology* 22: 305–315.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Average daily temperatures and cumulative precipitation for the 2011 growing season (1 April 2011–31 October 2011) compared to 20-yr averages.

Table S1 Matrix of Pearson correlation coefficients of soil parameter values